PROC. R. SOC. VICT. vol. 98, no. 2, 73-86, June 1986

THE VEGETATION ECOLOGY OF A COASTAL SAND DUNE IN SOUTH-EASTERN AUSTRALIA: GUNNAMATTA BEACH

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Abstract: The vegetation of Gunnamatta Beach, Victoria, is described in a series of topographic/vegetation units that generally agree with a numerical classification. Probable successional sequences are postulated, but spatial pattern appears to be determined largely by disturbance and concomitant erosion. Of the soil factors investigated only soil organic matter content seemed to coincide with the vegetation pattern; no correlation with salt spray was observed.

Ecological studies on coastal sand dune plants in Australia have received surprisingly little attention, although sand dunes cover a sizeable proportion of the long coastline. What studies there are have concentrated on only a few aspects (Osborn 1922, Patton 1934, Burges & Drover 1953, Smith 1957, Turner, Carr & Bird 1962, Parsons 1966, Parsons & Gill 1968, Harty & McDonald 1972, Robin & Parsons 1976, Batianoff & McDonald 1980, Moore 1980, Barson & Calder 1981). This present work is a local synthetic study of vegetation pattern, soil characteristics, succession and more importantly the habitat factors which apparently influence species distribution (Sacheti 1983). The work was carried out on a dune complex at Gunnamatta Beach, Victoria.

STUDY AREA

Situation

Gunnamatta Beach (Fig. 1) forms the south-eastern part of the Nepean Peninsula (lat. 38°25'S. long. 144°48'E). This Peninsula covers about 72 km² of mainly dune material. It lies between King Bay (Bass Strait) on the south and Port Phillip Bay on the north, its western extremity being Pt Nepean. In the east it extends to the scarp of Selwyn Fault, near Cape Schanck (Keble 1968). The front dunes of this beach run approximately south-east, parallel to the coast.

Geology and Geography

The Nepean Peninsula now consists largely of hummocky dune terrain, with some active dunes and others which are relatively stable beneath vegetation (scrub, woodland or grassland). The sand of these superficial Holocene dunes is mainly calcareous with about 25% quartz (Keble 1968); underneath there are Pleistocene dune sandstones. The present topography of Gunnamatta Beach is that of highly complex dunes whose irregularity is partly the result of past disturbances and more recently intensive recreational use.

History

Some evidence suggests that the study area was once covered by woodland—probably *Casuarina, Eucalyptus* and *Acacia* (Powell 1967). Aborigines of the Bunurang tribe inhabited this part of Victoria and it has been suggested that they used different plant parts for food (Brough Smyth 1878, Keble 1928) and used fire for cooking and hunting. Bird (1975) has remarked that natural vegetation was probably altered by the fires set by the aborigines whose kitchen middens can still be seen along the shores of the Nepean Peninsula. At Gunnamatta, some middens are on the mouth of the big blow-outs, although there is no evidence that links the origin of these blow-outs to the middens. Studies by Keble (1928), Daley (1931) and Calder (1974) suggest that little damage was done to vegetation by these natives even after inhabiting the areas for 30-40,000 years. Most of the damage/disturbance has been caused by European settlers. Evidence (Report of Senior Land Inspector to the Secretary for Lands, October 1945) suggests that Gunnamatta Beach (at that time known as part of Parish of Fingal) was then used by military forces, and this probably damaged the whole dune system. Even now, in most parts of Gunnamatta, abundant fragments of shrapnel are found in old bomb craters, and plant colonization in some of these sites (e.g. sandy plains) is very slow. More recently, much damage and erosion can be attributed to the large number of visitors and their motor vehicles, including trail bikes and dune buggies, despite attempts by the National Parks Service to protect the dunes (Bird 1975).

Climate

The climatic summary is based on data (1962-80) collected at Cape Schanck situated about 2.5 km south-east of Gunnamatta and corresponds to the Do type of Trewartha (1968): temperate-oceanic-humid with moderate summer and mild winter and adequate rainfall at all seasons. There is little seasonal variation in diurnal temperature range with average daily minimum of 11°C and maximum 17°C. Mean daily temperature maxima vary from 12.2°C in July to 21.9°C in February and mean daily minima from 7.6°C to 14.9°C. Because of a buffering maritime influence, Gunnamatta very rarely experiences prolonged hot weather (above 35°C). Rainfall occurs throughout the year, but there is considerable monthly variation (Fig. 2), the wettest and the driest months being May (84 mm) and January (40 mm), respectively. Nearly 57% of the average rainfall of 741 mm occurs in winter and spring. As with other Victorian coasts, westerly winds predominate, but with great diurnal variation in direction. Mean monthly wind speed varies from 10-30 km/hour and winds above 40 km/hour occur on 3-8 days per month, the higher frequency being in winter. Relative humidity is moderately high throughout the year (Table 1), but with some seasonal variation. Fog and frost are rare with less than five fog days per year, and frost recorded only six times in the last nineteen years.

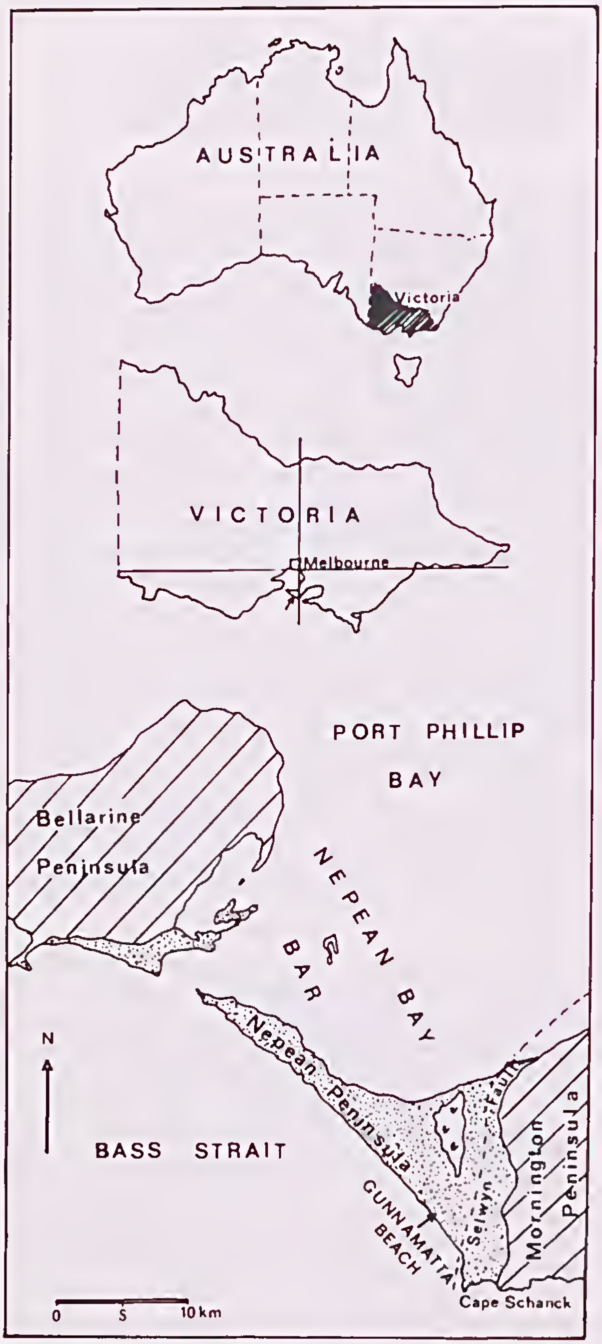

Fig. 1—Location of study area: Gunnamatta Beach, Victoria, Australia. (Simplified map after Bird 1975).

METHODS

Vegetation Analysis

The irregular and complex topography and lack of any chronological sequence with respect to distance from the shore make the choice of method for analysis difficult. From preliminary investigations it appeared that the vegetation pattern could be most easily studied by dividing the whole area into various combined topographic/vegetation units (dune habitat and community combinations) categorised principally (Fig. 3) on the basis of height/depth of topography, exposure and shelter, mobility/stability of the substratum. These units support different vegetation types, each characterized by a particular assemblage of dominant species of high constancy, although associated species may vary greatly. A

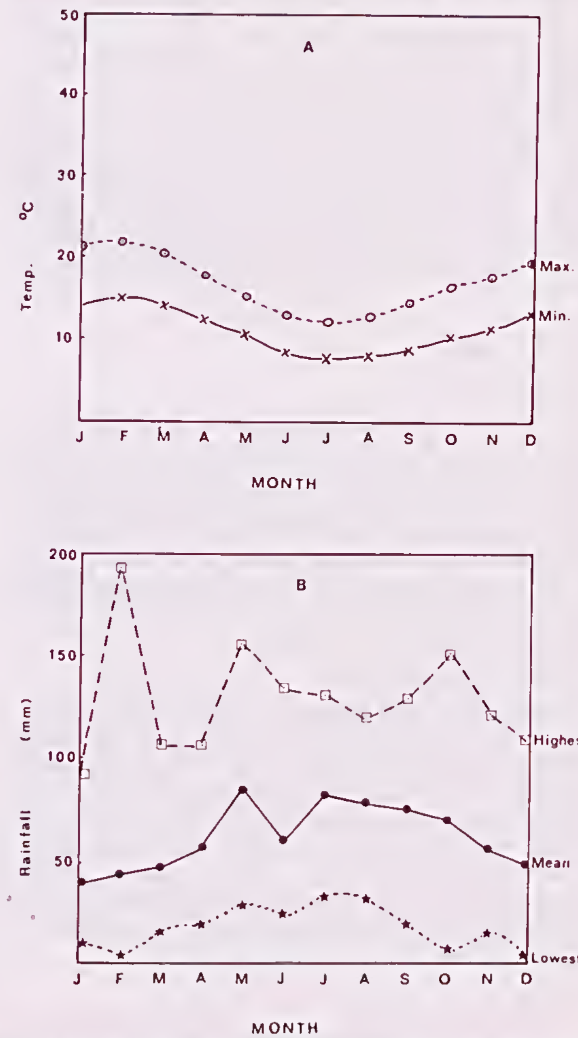

Fig. 2—(A), Average monthly maximum and minimum temperatures. (B), Average monthly, highest and lowest rainfall. (Based on data from Cape Schanck station; 1962-1980).

TABLE 1
SEASONAL VARIATION IN TEMPERATURE, RAINFALL AND RELATIVE HUMIDITY AT GUNNAMATTA (1962-1980)

Season	Temp. (°C) Max.	Min.	Mean	Rainfall (mm) Max.	Min.	Mean	R. humidity (%) 9 am	3 pm
Summer	21	13.9	17.5	266	52	132	75	70
Autumn	17.9	12.3	15.1	284	94	186	78	71
Winter	12.7	8.0	10.4	318	150	221	84	77
Spring	16.2	10.1	13.1	318	85	202	77	73

natural community nomenclature was thus used (Burnett 1964), which is slightly different from, and more descriptive than, most common dune terminologies. This was considered important in order to cater for the apparent complexity of the dune system without prejudicing its interpretation. To provide an independent check on the correspondence between subjectively determined (topographic) units and vegetation, three random transects were taken from shore to inland [recording cover/abundance in quadrats (50 × 50 cm) on a 4-point scale] crossing many, although not all, topographic units. These quadrats were then subjected to a classification procedure (HISNOB, polythetic divisive using a hierarchic information statistic; Boulton & Wallace 1970, 1973) and Ordination (GOWER ordination on a similarity matrix based on Sørenson's coefficient; Williams 1976). In addition, the vegetation of each unit was recorded at three sites selected for similarity. In each, quadrats (50 × 50 cm) were located by random co-ordinates (Greig-Smith 1964) and frequency, cover and density recorded in both winter (May-June) and summer (November-December) of 1980, recording 1,335 quadrats in all. The vegetation description of a few units was based only on observations. The nomenclature of plant species is based on Willis (1970, 1972).

Soil Analysis

From each topographic/vegetation unit, 5-10 soil samples were collected at 10 cm depth by soil borer. Each sample, consisting of five separate borings thoroughly mixed, was sealed in a polythene bag. Part of each was weighed, oven-dried at 80°C for 24 hours, cooled in a desiccator, re-weighed to give moisture content, then sieved (0.5 mm), and used for analysis: (1) Carbonate content estimated by Collins Calcimeter (Black 1965) and reported as percentage calcium carbonate by weight; (2) Soil pH and conductivity measured on a 1:5 soil water extract, determined by EIL pH meter (7050) with glass electrode, and portable conductivity meter type MC3 (Electronic Instruments, Ltd.); (3) Particle size analysis by sieving (Bagnold 1941); (4) Water-holding capacity (WHC) estimated by the Keen-Raczkowski method (Piper 1944, p.82) using small tubes of known diameter and expressed as a percentage of oven dry weight; and, (5) Soil organic carbon content estimated by a slightly modified Walkley and Black method (Piper 1944; Metson 1971).

Salt-Spray Analysis

Relative input of air-borne salt was assessed as by Oosting and Billings (1942) and Boyce (1954). A 5 × 5 cm cut-out in a 15 × 25 cm polythene bag exposed a 6 × 6 cm piece of Kleenex Industrial Tissue fixed by small strips of removable tape. From each tissue four such squares were made, one of which, in an unperforated bag, was used as control. In this way there were four controls for nine salt traps. This was necessary as the indigenous salt content varies appreciably in different tissues. The traps were placed 10 cm above and parallel to the ground and exposed to the wind for five hours. After exposure, the tissues were transferred, using forceps, to numbered glass vials, each shaken in 30 ml of distilled water for one hour and Na^+, K^+ and Ca^{++} measured by atomic absorption spectrophotometry (Varian Techtron).

VEGETATION COMPOSITION (See Table 8)

CORRESPONDENCE BETWEEN VEGETATION AND TOPOGRAPHY

Although GOWER has not separated the quadrats into groups as sharply as was considered possible in the field, the vegetation ordination is consistent with subjective classification into topographic units, and HISNOB classification is also consistent with it, although greatly simplified (Fig. 3).

Dunes

These have been considered under three broad categories and further divided into different topographic units, depending upon their origin, situation (distance from sea), mobility/stability of the substratum.

Front dunes: (a) Embryo (b) Initial (c) Old (Formerly Established).
Middle dunes: (a) Mobile (b) Fixed.
Rear dunes.

Front Dunes These, the most seaward line of dunes parallel to the coast, have been further divided into three types:

(a) *Embryo Dunes*: These small 'pre-dunes' or localized depositions of sand, present above High Water Mark but below the initial front dunes, vary in height from 0.5 to 1.5 m and are constantly subjected to erosion by sea and wind and trampling. In spite of this, some species, notably *Cakile maritima* and *Agropyron junceum*, not only survive but are able to form small dunes. The only

TABLE 2

NUMBER OF SAMPLES, RANGE AND MEAN VALUES OF VARIOUS SOIL FACTORS IN WINTER AND SUMMER IN TOPOGRAPHIC UNITS AT GUNNAMATTA. FIGURES IN PARENTHESES INDICATE THE SUMMER VALUES WHILE PRECEDING FIGURES ARE WINTER VALUES.

Topographic Unit	No. of Samples	$CaCO_3$(%)*	pH	O.C.C. (%)	Conductivity (μmhos)	Water Holding Capacity (%)	Dominant Vegetation Type
Front Initial Dunes	15	Mean 22.0 Range 20.0-23.9	8.2 (8.4) 8.1-8.4 (8.3-8.5)	0.135 (0.154) 0.110-0.165 (0.130-0.185)	96 (137) 82-115 (95-155)	21.6 21.1-22.4	*Spinifex-Agropyron*
Mobile Dunes	15	Mean 24.3 Range 21.9-27.4	8.9 (8.8) 8.8-9.4 (8.7-8.9)	0.159 (0.163) 0.138-0.178 (0.145-0.198)	93 (84) 75-120 (70-100)	22.2 21.8-22.8	*Ammophila*
Fixed Dunes	20	Mean 21.9 Range 20.6-22.6	8.2 (8.5) 7.9-8.7 (8.1-8.8)	0.298 (0.308) 0.199-0.386 (0.168-0.481)	85 (81) 75-100 (70-100)	24.7 24.5-25.2	*Spinifex-Ammophila* (old) & Shrubs (annual in summer)
Craters	15	Mean 21.3 Range 20.2-22.6	8.3 (8.5) 8.1-8.6 (8.2-8.7)	0.315 (0.320) 0.195-0.393 (0.199-0.437)	105 (86) 90-125 (70-98)	24.1 23.4-24.6	*Spinifex* (old) -*Scirpus* & shrubs (annuals in summer)
Clefts	25	Mean 20.7 Range 18.9-22.0	7.9 (8.0) 7.5-8.3 (7.9-8.6)	0.474 (0.500) 0.364-0.689 (0.313-0.893)	91 (86) 80-100 (75-102)	25.8 25.4-26.0	Shrubs (annuals in summer)
Rear Dunes	10	Mean 19.7 Range 18.4-20.3	7.7 (7.8) 7.4-7.8 (7.7-8.0)	1.93 (1.97) 1.60-2.76 (1.41-2.80)	132 (142) 120-150 (105-175)	32.5 31.5-33.8	*Leptospermum* closed scrub (annuals in summer)

* Analysis not carried out for summer

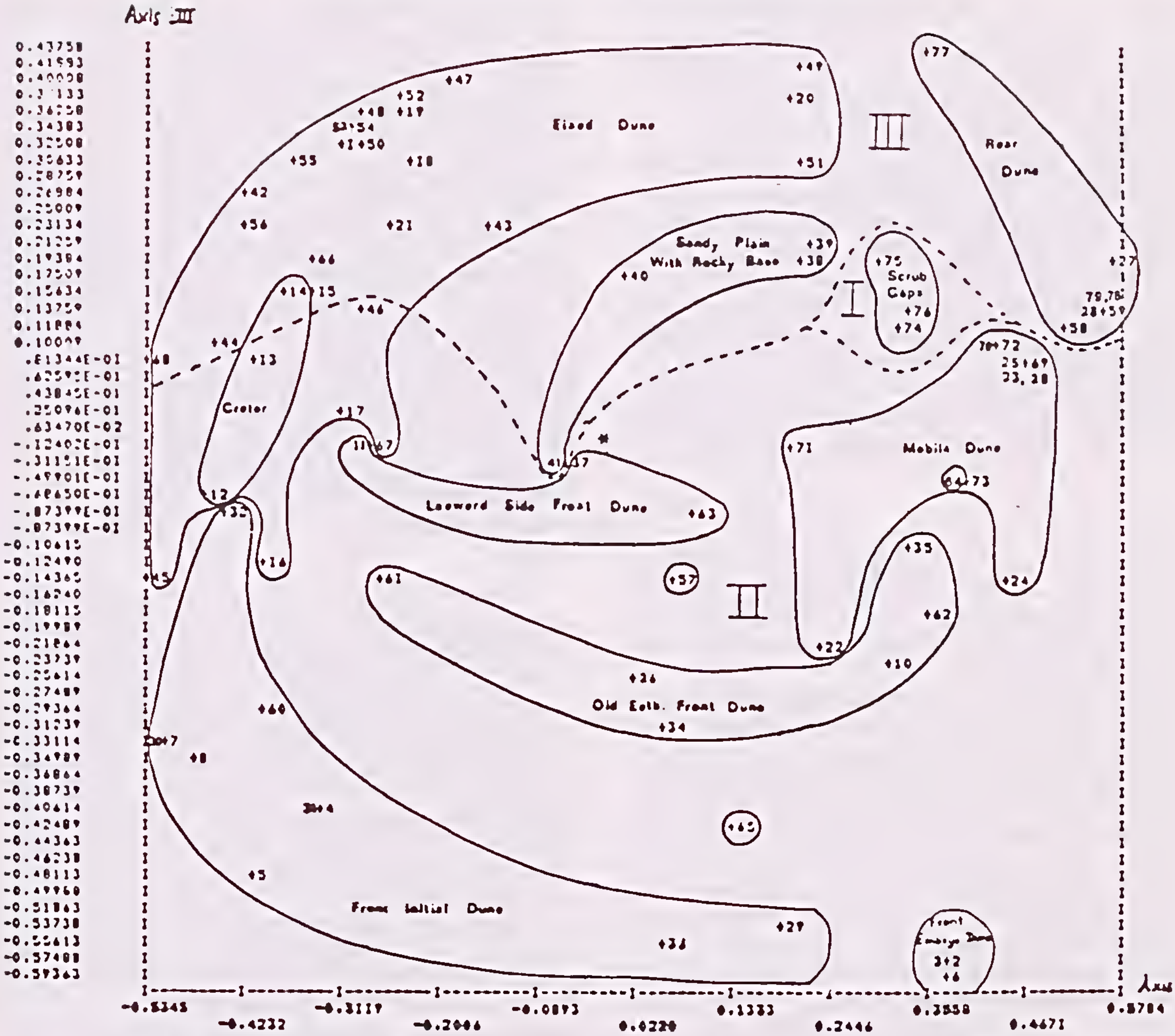

Fig. 3 – Scatter diagram of quadrats produced by computer analysis of data of transects using Gower ordination. Group I, II and III produced by HISNOB.
* Represents seven empty quadrats from Sandy Plain.

other species able to survive hereabouts are the grasses *Spinifex hirsutus* and *Ammophila arenaria*, although *Spinifex* seedlings, observed on the beach during summer, did not survive for long and do not appear to contribute to the formation of these dunes.

Embryo dunes have $CaCO_3$ and organic carbon content values similar to those of initial dunes (Table 2).

(b) *Initial Dunes*: These, the main line of recently-formed front dunes, are flat, 4-20 m wide, of moderate height (1-4 m), generally discontinuous and run parallel to the coast. They are always subjected to wind borne salt, sand, and continual pressure of visitors. Some species, however, gradually build up the dunes and stabilize the substratum, in particular *Spinifex hirsutus* and *Agropyron junceum*, the former being dominant. At Gunnamatta, *Ammophila* either does not occur on initial front dunes or, where present, is found only in localised patches. The two other common species are *Cakile maritima* and *Festuca littoralis*. Rarely, a few plants of *Senecio lautus* or *Helichrysum paralium* (small plants) also occur.

Initial dunes show some variation in soil features, and are characterized by low organic matter in the soil with a high pH and $CaCO_3$ content (Table 2). The particle size varies from medium to fine grade of sand, with 5% coarse sand.

(c) *Old Established Dunes:* These, the most massive of the front dunes, are 6-10 m high and characterized by generalized erosion, particularly on the seaward sides or blow-outs. In some places, particularly on the eastern end of the Gunnamatta complex, in the absence of embryo and initial front dunes, established dunes form the first line next to the sea and are typically dominated by old woody *Helichrysum paralium*, with dry, dead branches towards the sea and green sloping branches to leeward. Most noticeable is the complete absence of

Agropyron. Other common plants here include *Spinifex, Ammophila, Cakile*; occasionally *Senecio lautus, Scirpus nodosus* and, in places, *Stackhousia spathulata, Calocephalus brownii* and *Melilotus indica* (always under some sort of shelter).

The dune soils are very varied.

(d) *Leeward side of front dunes*: Although not treated here as a separate topographic unit, these stands have tended to segregate out together on Axis III of the ordination (Fig. 3) and constitute a borderline category which would have been worth recognising at a slightly finer resolution. The pattern of vegetation is very diverse, differing every 30-40 m. The plant communities generally dominating are: *Spinifex-Ammophila* or *Helichrysum-Scirpus-Ammophila* or *Spinifex-Festuca-Ammophila*. The other common plants are *Senecio, Stackhousia, Calocephalus, Melilotus* and *Lagurus ovatus* (summer only).

Middle Dunes

One of the most striking topographic units at Gunnamatta, these are characterized by a great variety of dunes—from small to very high (~ 30 m), young and old (although evidence for the real age of such dunes could not be established).

(a) *Mobile Dunes*: This unit most clearly demonstrates the effects of disturbances to formerly established dunes, resulting in complete degradation of vegetation and ensuing erosion. Some such dunes are among the highest at Gunnamatta and are highly mobile and are now dominated by *Ammophila*; exclusively at initial colonization. The consequence of disturbance is clearly seen in the change of pioneer plant species; *Spinifex*, the primary colonizer of initial front dunes, here becomes secondary and establishes itself only after *A. arenaria* has stabilized the substratum to some extent. Despite the mobility, *Festuca littoralis*, common on initial dunes, grows here at only one site. Small numbers occur of *Cakile*, *Senecio* and *Melilotus* although only where sheltered by *Ammophila* plants; as well as a few plants of *Scirpus* and *Stackhousia*, particularly on small dunes 4-5 m in height.

The mobile dunes, always subjected to fresh wind-blown sand, have the highest carbonate content, up to 27.4%, and high pH (Table 2). They have higher organic matter than front initial dunes and moisture content higher than any topographic units, except rear dunes.

(b) *Fixed Dunes*: These differ from the mobile dunes, in topography and vegetation, but most noticeably in the substratum which is almost static except for a slight deposition of wind blown sand. They are very irregular in outline, commonly eroding over the surfaces facing the sea, or by localised blow-outs. The vegetation pattern is compact and diversified. Most of these dunes at Gunnamatta are still dominated by grasses—*Spinifex* and *Ammophila*—although with a marked change in growth form and vigour, here present only as moribund colonies. Although shrubs are abundant they are too scattered at this stage to form a distinct shrubland in their own right. The main shrubs vary from dune to dune. Those commonly found are: *Acacia longifolia* var. *sophorae, Pimelea serpyllifolia, Helichrysum paralium, Leucopogon parviflorus, Leptospermum laevigatum* and less frequently *Olearia axillaris*. At most places these shrubs are low (2-3 m). The presence of *Melilotus indica* and *Lagurus ovatus* in large numbers (up to 600 plants per m^2) during summer is striking. Other plants include: *Senecio lautus*—host of the only parasitic plant, *Orobanche minor*—*Stackhousia spathulata, Scirpus nodosus, Swainsona lessertiifolia* and *Carpobrotus aequilaterus*. The appearance of *Clematis microphylla, Apium prostratum, Acaena anserinifolia* and colonies of mosses can clearly be linked with the amelioration in habitat: increase in organic matter, substrate stability and the shelter afforded by shrubs. In winter, fungi (*Hygrophilus* spp.) and algae (*Nostoc* spp.) are also found. Carbonate content of soil is still very high (21.9%) and pH values show a great variation (7.9-8.7); surprisingly the soils here have the lowest conductivity values (Table 2).

Craters

These are rather flat, bare and exposed in the middle and surrounded by dunes of varying height, thus resembling enclosed amphitheatres. They mostly occur behind the front dunes and between or behind the middle dunes. The substratum is relatively stable, the loose sand having been removed by explosions frequently exposing a former, harder soil surface; but some craters are situated near the shore and hence receive substantial amounts of salt-spray and fresh-blown sand. Although much more sheltered than fixed dunes, craters are less diversified in vegetation, dominated by a *Spinifex* (old plants)—*Scirpus* community, *Ammophila* being present only in patches. The shurbs (1-2 m tall) commonly found here are—*Helichrysum, Leucopogon, Calocephalus* and occasionally *Acacia, Pimelea* and *Olearia*. Of the annuals, *Melilotus* is more frequent than *Lagurus* during summer. Perennials include: *Senecio, Stackhousia, Carpobrotus* and occasionally *Swainsona*. Mosses also occur, especially under the shrubs.

There is little difference in soil characters compared with fixed dunes, most notably a higher conductivity; a slight increase in organic matter content (Table 2) and moisture content, may not be significant.

Clefts

These are narrow sheltered areas which lie mainly between the middle dunes, mobile or fixed, and in places demonstrate the vegetation pattern prior to disturbances. Most appear to have been formed as a result of the building up of dunes around them, rather than by excavation. Being sheltered, they generally receive negligible wind-blown salt-spray and sand. The diversity in vegetation, and the presence of even mesophytic species in some clefts, clearly indicate significant differences in habitat conditions from other parts of Gunnamatta. The plant species show an inter-mixture of original and recent vegetation and include some species not found elsewhere. The vegetation at most places is dominated by shrubs such as *Leptospermum laevigatum* (mostly old plants), *Acacia longifolia* var. *sophorae, Leucopogon parviflorus, Pimelea serpyllifolia* and *Olearia axillaris*. The *Spinifex–Ammophila* community is present, mostly as relicts, with a greatly reduced cover, whereas *Scirpus nodosus* is more frequent, although it covers less area, and *Carpobrotus aequilaterus* is common. Other plant species regularly found, though scattered, are: *Swainsona lessertiifolia, Stackhousia spathulata, Senecio lautus, Orobanche minor, Sonchus megalocarpus* and—in some of the clefts—*Dichondra* spp., *Apium prostratum, Acaena anserinifolia. Kennedia prostrata*, very restricted at Gunnamatta, is found in some clefts. In summer, *Lagurus ovatus* is the most frequent and abundant annual with *Melilotus indica* not quite so plentiful. Mosses here cover a much greater ground area, again indicating different habitat conditions.

A slight decrease in carbonate and pH with an increase in organic matter and moisture content (4.1%) is observed, but the soil is still very rich in $CaCO_3$ and is still alkaline (Table 2).

Rear Dunes

This unit, which supports the present-day final stabilized community, is dominated by *Leptospermum* closed-scrub which, prior to disturbance, apparently extended to near the sea as indicated by the presence of isolated old individuals throughout Gunnamatta, particularly on the eastern side, close to the shore. The closed-scrub, in general, lacks any understorey vegetation, except in areas where light is not the limiting factor. Two old trees of *Banksia integrifolia* in one locality, perhaps point to the possibility of a formerly more complex woodland. Epiphytic lichens and the liverworts *Frullania* spp. and *Austrolejeunea nudipes* (Hook. f. and Tayl.) Grolle, indicate a surprisingly humid microclimate within this community type.

A decline in $CaCO_3$ content, pH and increase in organic matter is observed, but the soil still does not show any profile differentiation (Table 2).

Blow-Outs

The formation of this topographic unit, a common feature of Gunnamatta, is clearly associated with past disturbances. Although it is impossible to determine the origins of the disturbances, the evidence suggests that natural and man-made activities (trampling, vehicles, military and perhaps aboriginal activities) are likely to be responsible for the degradation of the vegetation and, consequently, initiation of blow-outs. Some blow-outs are extensive, up to 150×70 m. The leeward sides develop into parabolic dunes, of which some are large and mobile, the great mobility apparently hindering colonization. Although conditions for growth are very stringent, some species, mainly *Ammophila, Spinifex* and *Cakile*, are able to survive, and in places on the leeward side, *Spinifex* and *Ammophila* grow very luxuriantly. Surprisingly, some blow-outs are among the very few sites where seedlings of both *Ammophila* and *Spinifex* have been observed during summer. Very rarely, young plants of *Helichrysum* occur.

In soil characteristics, the blow-outs are very similar to mobile dunes.

Sandy Plains

These are flat and exposed, like craters, but covering a very large area, and can be situated either close to the shore or adjacent to the inland vegetation. Their formation is further evidence of disturbance by military activities; where, even after more than 40 years, fragments of bullets and shrapnel can be found on the surface. The plains are either devoid of any vegetation or, in some places, *Ammophila* and *Spinifex* occur round the edges slowly advancing towards the centre. Colonization appears to be very slow because of limited supply of fresh sand and, at present rates, it will take decades, if not centuries, before these areas are colonized completely.

Seedlings of *Spinifex, Ammophila* and *Melilotus* have been observed but none survived.

Miscellaneous Units

(a) *Sandy Plain with Rocky Base*: This topographic unit, found at only one place in Gunnamatta between a front and middle dune, is common on adjacent coasts. It is characterized by the presence of rhizoconcretions and limestone rock beneath a thin covering (30 cm) of bare sand. The vegetation is typically very uniform, open, and dominated by a *Calocephalus-Scirpus* community. *Ammophila* is totally absent, and *Spinifex* is present only in small patches. *Stackhousia* is the most frequent annual. Other commonly occurring plants are *Carpobrotus, Senecio* and, during summer, *Melilotus*. Small shrubs of *Helichrysum paralium* are also present, but are very scattered.

(b) *Dune Hollows Rich in Organic Matter*: These are small hollows, more or less surrounded by old *Leptospermum* shrubs. The substratum is relatively rich in organic matter, and receives almost no supply of wind-blown sand or salt-spray. The most abundant plant is *Swainsona*, particularly near the margins of *Leptospermum* patches. *Carpobrotus* and *Senecio* are the most frequent perennials and during summer *Melilotus* and *Lagurus* occur in large numbers. Both *Ammophila* and *Spinifex* are present, but only as relicts. Mosses cover a substantial proportion (>45%) of the ground area.

(c) *Scrub-gaps*: These are small gaps formed as a result of some sort of disturbance, especially to the aerial parts of *Leptospermum* closed-scrub, leaving behind old woody stems. The substratum is fully stabilized because of relatively high amounts of organic matter in the soil, but being exposed they receive some blown sand. This topographic unit demonstrates a completely different vegetation pattern, the distinctive feature being the presence of mosses such as *Barbula torquata* and *Tortella calycina* covering almost 70% of the ground area. Other noticeable features are the presence of *Swainsona, Senecio* and *Leucopogon* as the most common plants, and the complete absence of all pioneer species. Other species found here are—*Pimelea serpyllifolia, Stackhousia spathulata, Scirpus nodosus, Carpobrotus aequilaterus, Melilotus indica* and *Lagurus ovatus* (in summer).

PATTERN IN TIME AND SPACE

The complexity and irregularity in topography, further aggravated by the lack of any fixed relationship of topographic units with distance from the sea, are clearly evident in the vegetation pattern which seems, at first glance, to exemplify anarchy rather than causality. There is no obvious logical pattern in topography and vegetation, but rather a mosaic of vegetation which is complex and apparently irrational. Plant communities growing immediately adjacent to each other may belong to pioneer and final (stabilized) stages, a vegetational paradox typical of Gunnamatta. Nor do the shrub communities demonstrate any consistent pattern and different species combinations are found at different sites even of the same topographic unit. This floristic diversity within an apparently homogeneous habitat is unpredictable and presumably reflects different origins, ages (time since stabilization), and habitat development. An ecologically significant feature is the change in vegetation pattern, resulting from disturbances. For example, on mobilised middle dunes *Ammophila* becomes the first colonizer instead of *Spinifex*. Similarly in scrub-gaps, *Swainsona, Senecio* and *Leucopogon* are the first colonizers; normally these plants appear during the second phase of succession.

From the soil analysis (Table 2) it is apparent that soil at Gunnamatta is calcareous and still alkaline in all topographic units. There is slight decrease in the amount of calcium carbonate, from 24.3% (mobile dune) to 19.7% in the rear dunes, perhaps because of initial high $CaCO_3$ and incomplete leaching. In this respect Gunnamatta shows a similarity to the highly calcareous dunes of the Outer Hebrides (Gimingham 1951). Although the soil is still alkaline even in older topographic units (rear dunes) it shows a pattern of general decrease with age (stabilization). There is, however, no constant relationship of pH decrease with increase in distance from sea. As in other dune systems (Salisbury 1922, 1925, Gimingham 1951), the sands are initially poor in organic matter but this increases significantly in the later stages of succession. Soil salinity is negligible in most of the topographic units, because most of the salts are washed away by rain.

Relationship of topographic units and soil factors

Of the several factors investigated—$CaCO_3$, pH, organic carbon content, conductivity, moisture content, soil particle size—only soil organic carbon content shows any kind of consistent relationship with different vegetation types. Water Holding Capacity is closely-related to organic carbon content, as would be expected. In topographic units where soil organic carbon content is low (<0.17%), vegetation mainly consists of pioneer plant species (*Cakile, Spinifex, Agropyron, Ammophila*) (Table 2); but, where the soil organic carbon content exceeds *c* 2% it is mainly dominated by *Leptospermum* closed-scrub. With intermediate values of soil organic carbon content, the vegetation varies.

Species Distribution at Gunnamatta

The complex vegetation pattern at Gunnamatta has no apparent overall consistency, but some species (e.g. *Melilotus indica, Senecio lautus*) are widely distributed while some others (e.g. *Agropyron junceum, Cakile maritima*) are restricted. An attempt was therefore made to determine whether there were habitat factors controlling, limiting or at least correlated with the distribution of individual species, rather than vegetation. Several probable factors (Table 3), some of which have been shown to be the major controlling/limiting factors in other dune systems [salt-spray (Oosting & Billings 1942, Martin 1959, Parsons & Gill 1968, Randall 1974, Barbour 1978); pH (Burgess & Drover 1953, Böcher 1954)], were considered in some detail. Other factors, such as precipitation, air temperature, light and wind, were felt to affect the overall vegetation, generally

TABLE 3
VARIOUS HABITAT FACTORS CONSIDERED IN DIFFERENT AREAS FOR VEGETATION ZONATION / SPECIES DISTRIBUTION

Factors	Area	Authors and Year
Wind	East Mediterranean Coasts, Israel	Zohary & Fahn (1952)
Salt-spray	Bogue Bank, N. Carolina, U.S.A.	Oosting & Billings (1942)
	East Mediterranean Coasts, Israel	Zohary & Fahn (1952)
	Island Beach State Park, U.S.A.	Martin (1959)
	Wilson's Promontory, Victoria, Australia	Parsons & Gill (1968)
	Monach Isles National Nature Reserve, Outer Hebrides	Randall (1974)
Sandmovement/ substrate stability	Coastal sandy shores, Japan	Nobuhara (1967)
	Cape Hatteras National Seashore, U.S.A.	Van der Valk (1973)
	Donana National Park, Spain	Garcia Nova (1979)
Moisture content	Eastern Cape Coast, South Africa	Lubke & Avis (1982)
Water-table	Braunton Burrows, U.K.	Willis *et al.* (1959)
Particle-size	Greek Coasts, Greece	Lavrentiades (1975)
Soil salinity	Barbados Coast, Barbados	Gooding (1947)
pH	European coasts, Europe	Böcher (1954)

TABLE 4
pH RANGES OF MAIN SPECIES AT GUNNAMATTA (RESULTS BASED ON 30-60 SAMPLES FOR EACH SPECIES)

Species	pH range
Acacia longifolia var. *sophorae*	7.9-8.7
Agropyron junceum	7.6-9.1
Ammophila arenaria	8.0-9.4
Cakile maritima	7.5-9.0
Calocephalus brownii	7.5-9.1
Carpobrotus aequilaterus	7.6-8.9
Festuca littoralis	8.0-8.8
Helichrysum paralium	7.8-8.6
Kennedia prostrata	7.4-8.9
Lagurus ovatus	7.6-8.5
Leptospermum laevigatum	7.4-8.6
Leucopogon parviflorus	7.4-8.4
Melilotus indica	7.6-9.0
Olearia axillaris	7.6-8.9
Pimelea serpyllifolia	7.7-8.5
Scirpus nodosus	7.5-8.9
Senecio lautus	7.5-8.8
Spinifex hirsutus	7.7-9.1
Stackhousia spathulata	7.7-9.2
Swainsona lessertiifolia	7.5-9.0

without a significant local effect. The factors—particle size, moisture content, sand movement and soil salinity—were not found to be major factors limiting the occurrence of species to particular dune habitats although, on a much smaller scale, they may influence the distribution of individual plants, especially during the germination/early establishment phase. Soil pH (Table 4) was also found to have no correlation with the occurrence of particular species. Salt-spray, considered to be a major causal factor of vegetation zonation/species distribution in different parts of the world by various workers (Table 3), was also investigated in detail, but results (Table 5) showed that no gradient in salt deposition was observed at Gunnamatta, and no vegetation pattern corresponded to the pattern of deposition of salt. Salt-spray, therefore, cannot be considered a major or decisive factor influencing the spatial distribution of plant species, although it has been observed to influence some species by killing seedlings during sudden blasts of salt-spray or by damaging the shoot apex/leaves of some plants especially on front dunes. The pattern of influence, however, is neither predictable nor, *a posteriori*, discoverable.

The correlation observed between vegetation and soil organic carbon content (O.C.C.) may be interpreted as evidence of either a cause or an effect of the presence of particular species. Since O.C.C. was the only factor which showed any kind of direct relationship with different vegetation types, the hypothesis was made that O.C.C. could be a factor correlated with, or even determining, species establishment at particular sites. This was first investigated with *Cakile maritima* and then extended to 18 other species (Sacheti 1981). Each species is associated with a particular O.C.C. range, sometimes rather narrow (Table 6). Species with narrow ranges (<20% of the total range) are generally confined to localities with low O.C.C., and have a restricted distribution; species with medium, wide and full ranges have a moderate to wide distribution. Species with narrow ranges are pioneers and early colonizers of dune

TABLE 5
DISTRIBUTION OF CATIONS AT TWELVE DIFFERENT SITES (ppm/cm^2)

Wind Direction		SE			SW			NE			NW	
Site No.	Na^+	Ca^{++}	K^+	Na^+	Ca^{++}	K^+	Na^+	Ca^{++}	K^+	Na^+	Ca^{++}	K^+
1.	0.041	0.031	0.002	0.095	0.030	0.004	0.072	0.024	0.006	+	+	+
2.	0.115	0.031	0.002	0.071	0.025	0.003	0.045	0.038	0.008	0.050	0.012	0.004
3.	0.125	0.055	0.005	0.071	0.033	0.003	0.037	0.024	0.008	0.060	0.019	0.021
4.	0.050	0.024	0.001	0.011	0.028	0.004	0.029	0.020	0.010	0.056	0.018	0.018
5.	0.036	0.017	0.001	0.053	0.034	0.004	0.041	0.020	0.009	0.022	0.009	0.005
6.	0.066	0.031	0.001	+	+	+	0.029	0.020	0.001	0.033	0.016	0.008
7.	0.043	0.022	0.001	0.180	0.031	0.004	0.039	0.015	0.016	0.045	0.015	0.012
8.	0.080	0.019	0.001	0.074	0.032	0.002	0.072	0.018	0.004	0.050	0.012	0.007
9.	0.087	0.029	0.001	0.217	0.039	0.008	0.128	0.086	0.006	0.062	0.019	0.012
10.	0.520	0.066	0.017	0.560	0.056	0.042	0.080	0.031	0.006	0.059	0.019	0.014
11.	0.087	0.024	0.001	0.463	0.061	0.045	0.119	0.024	0.051	0.048	0.022	0.019
12.	0.235	0.045	0.008	0.801	0.102	0.050	0.148	0.031	0.050	0.065	0.027	0.031

Brief description of the sites

1. = High Mobile Dune (near inland)
2. = Sandy plain (near inland vegetation)
3. = Eroding Dune (behind middle dune)
4. = Fixed dune (high; middle of Gunnamatta)
5. = Partly exposed crater (middle of Gunnamatta)
6. = Small sheltered dune hollow
7. = Small fixed dune (facing south)
8. = Cleft (surrounded by dunes)
9. = Open, exposed sandy plain (behind front dunes)
10. = Eroding face of dune (near sea)
11. = Leeward side of blow-out (near sea)
12. = Front Initial Dune

\+ Salt-traps removed by visitors

TABLE 6
O.C.C. RANGES OF MAIN SPECIES AT GUNNAMATTA

Species	O.C.C. Range (%)	Proportion of Total range (%)
Agropyron junceum	0.10-0.17	2.7
Spinifex hirsutus		
(young plants)	0.11-0.25	5.2
(old plants)	0.25-0.75	18.5
Ammophila arenaria		
(young plants)	0.10-0.26	5.9
(old plants)	0.26-0.97	26.3
Cakile maritima	0.10-0.28	6.7
Festuca littoralis	0.10-0.33	8.4
Stackhousia spathulata	0.12-0.60	17.4
Calocephalus brownii	0.11-0.62	18.6
Acacia longifolia var. *sophorae*	0.20-0.72	21.5
Helichrysum paralium	0.15-0.84	25.5
Kennedia prostrata	0.23-0.99	27.8
Olearia axillaris	0.22-0.99	28.6
Carpobrotus aequilaterus	0.15-0.99	30.7
Scirpus nodosus	0.16-1.09	34.4
Lagurus ovatus	0.19-1.46	47.0
Melilotus indica	0.15-1.43	47.4
Senecio lautus	0.14-1.51	50.7
Swainsona lessertiifolia	0.15-1.55	51.8
Pimelia serpyllifolia	0.23-1.66	52.8
Leucopogon parviflorus	0.20-2.68	91.5
Leptospermum laevigatum	0.22-2.80	95.4

succession, species confined to medium and wide ranges appear during the second stage of succession, and those corresponding to full range are co-dominants and dominants of the final stabilized stage (Table 7). Thus it appears that if O.C.C. is limiting (directly or indirectly), species with narrow ranges are the ones whose occurrence is most likely to be limited by the amount of organic carbon in the soil, whereas the distributions of species belonging to medium and higher ranges are likely to depend on several other factors as well, e.g. intolerance to burial and salinity (Sacheti 1983), substratum stability, soil temperature etc. The significance of O.C.C. ranges will be discussed in detail in a separate paper.

Seasonal Variation

Results of the vegetation analysis replicated in winter (May-June) and summer (Nov.-Dec.) suggest that there is little seasonal variation in the vegetation pattern—the only significant difference is in the presence, in summer, of the annuals *Melilotus* and *Lagurus* in large numbers in some of the topographic units, for example, fixed dunes, clefts, craters. Extensive data over at least 3-4 years would be required to detect and confirm significant changes taking place in perennial species. As would be expected, soil characteristics showed no detectable change (Table 2) in most factors investigated, although a slight increase in organic carbon content and pH was observed. Moisture content was the only factor which showed a difference in winter and summer values and that is a transient feature.

Succession

The results of two kinds of successional change (primary and secondary) can be observed at Gunnamatta, although the changes in vegetation with time can only be deduced from the patterns existing at present (Scott 1965). Aerial photographs do not span a great enough time, nor are they sufficiently detailed, to reveal what has actually happened. The conversion of bare sand, freshly provided by the sea, into woodland, is primary succession, and the re-working of rejuvenated older sediments, leading towards a similar result is considered to be secondary succession. The forces driving primary succession are autogenic, changes induced by the plants themselves modifying the habitat, whereas secondary succession, although similar in principle, is triggered by erosion. If the erosion is repeated, the succession may be more or less cyclical. "Disturbance creates patches of successional environments whose size depends on the type and severity of the disturbance" (Pickett 1976).

Disturbance has played a crucial role in the development of Gunnamatta into a complex dune system; hence it is almost impossible to locate even a small area which shows a series of successional stages in spatial and chronological order. Without dune ages, no rigid correspondence could be established between the age of the dunes and phases of succession. Thus succession can only be deduced by arranging the various stages of vegetation development in a logical sequence from areas of initial colonization of bare sand to the present-day final stage. The pattern deduced is subjective, but plausible, and corresponds to Connell and Slatyer's (1977) facilitation model I. Since, undoubtedly, disturbances have played an important role in the make-up of this area, it would be logical to consider the succession under two headings (see Fig. 4): 1. Undisturbed succession (Primary); and, 2. Disturbed succession (Secondary).

Undisturbed succession

In the absence of any major disturbance, this can still be observed in the far eastern part of Gunnamatta. It is similar to other Victorian dune systems although the dominant plant species are different. The important stages are:

(a) *Grassland stage*: This starts on front embryo/initial dunes with the colonization of bare, mobile sand, low in organic matter, by plant species such as *Cakile maritima, Spinifex hirsutus* and *Agropyron junceum*. By sand accumulation and continued survival in harsh conditions (e.g. windblown sand, salt-spray, mobile substratum, trampling) these plants gradually stabilize the sand enabling other species to become established. Other taxa, such as *Ammophila arenaria* and *Festuca littoralis*, arrive later and become important contributors to ameliorating edaphic conditions by increasing organic matter content (and, hence, water holding capacity) and stability. Eventually, however, the changed habitat conditions appear to become less suitable for the existence

Table 7

Distribution of Various Species at Gunnamatta

FED = Front embryo dunes; FID = Front initial dunes; OFD = Old established front dunes; LFD = Leeward side of front dunes; MD = Mobile dunes; FxD = Fixed dunes; RD = Rear dunes; Cr = Craters; Cl = Clefts; SG = Scrub gaps; DH = Organic matter rich dune hollows; BO = Blow outs; SP = Sandy plains; SPRB = Sandy plains with rocky base.

Species	O.C.C. Range	Distribution at Gunnamatta
Agropyron junceum	NARROW RANGE	FED, FID
Spinifex hirsutus		
(young plants)		FID, LFD, SP, MD, BO
(old plants)		FxD, Cr, Cl, DH
Ammophila arenaria		
(young plants)		MD, FID, LFD, SP, BO
(old plants)		FxD, Cr, Cl, DH
Cakile maritima		FED, FID, LFD, MD, SP, BO, OFD
Festuca littoralis		FID, LFD, Cr, MD, OFD
Stackhousia spathulata		SP, FxD, Cr, Cl, SPRB, LFD, DH
Calocephalus brownii		SPRB, SP, Cr, LFD
Acacia longifolia var. *sophorae*	MEDIUM RANGE	FxD, Cr, Cl, LFD, DH
Helichrysum paralium		OFD, FxD, Cr, Cl, SPRB, SG
Olearia axillaris		FxD, Cr, Cl, SG, DH, LFD
Carpobrotus aequilaterus		FxD, Cr, Cl, DH, LFD, SPRB
Scirpus nodosus		Cr, FxD, Cl, SPRB, SG, DH, LFD
Lagurus ovatus	WIDE RANGE	Cl, FxD, SG, DH, Cr, RD, LFD, SP, SPRB
Melilotus indica		FxD, Cl, Cr, DH, SG, RD, LFD, SP, OFD, SPRB, OFD, FED, MD
Senecio lautus		FxD, Cl, Cr, SG, DH, RD, LFD, OFD, SP, SPRB, FED, MD
Swainsona lessertiifolia		FxD, Cl, Cr, SG, DH, RD, LFD, OFD, SP
Pimelea serpyllifolia		FxD, Cl, Cr, RD, SG, DH, LFD
Leucopogon parviflorus	FULL RANGE	RD, Cl, FxD, Cr, DH, SG, LFD, OFD
Leptospermum laevigatum		RD, Cl, FxD, Cr, DH, SG

of these pioneers/early colonizers and the sites are then invaded by other plant species.

(b) *Old grassland/shrub community stage*: This is marked by a change in vegetation structure from being open, sparse and uniform to compact and diversified. The changes in habitat (reduced supply of fresh-blown sand, increase in organic matter content, competition with other plants) result in, or are accompanied by, the gradual decline, especially of grasses—*Spinifex hirsutus* and *Ammophila arenaria*—and the appearance of shrubs and annuals. At most sites this stage is still dominated by an old grass community of *Spinifex* and *Ammophila*, but is also marked by the presence of shrubs, mosses, and large numbers of *Melilotus* and *Lagurus* during summer. This second stage of succession, certainly the most diversified of all, would gradually lead to domination by shrubs and the decline and ultimate loss of most herbaceous species.

(c) *Closed-scrub stage*: The gradual decline of most grasses, herbaceous perennials, and annuals, and the corresponding rise to dominance of shrubs, bring about the final stage. Initially dominated by a variety of taller shrubs, later it comes to consist of *Leucopogon-Leptospermum* community and finally (as far as present vegetation goes) *Leptospermum* closed scrub.

Disturbed Succession

Except for the eastern end of Gunnamatta, the original vegetation dominated by *Leptospermum* closed-scrub has mostly been damaged (partially or totally), and the complete primary succession is scarcely evident. But this disturbance has resulted in opening new sites for secondary succession, most of which are similar to those associated with primary succession, in that colonization starts from bare sand, generally low in organic carbon (~0.15%), although in some sites, e.g. scrub-gaps, the substratum is relatively rich in organic matter (~0.44%). Secondary succession differs from primary mainly in the unpredictable course it follows. Probably in some sites it is similar to primary succession, but may never reach any stabilized stage or else the pattern may be altogether different. Whatever its direction, the pattern of secondary succession is likely to be of significance as an indicator for future management.

The main topographic units from which the secondary succession appears to have started are: (i) Re-

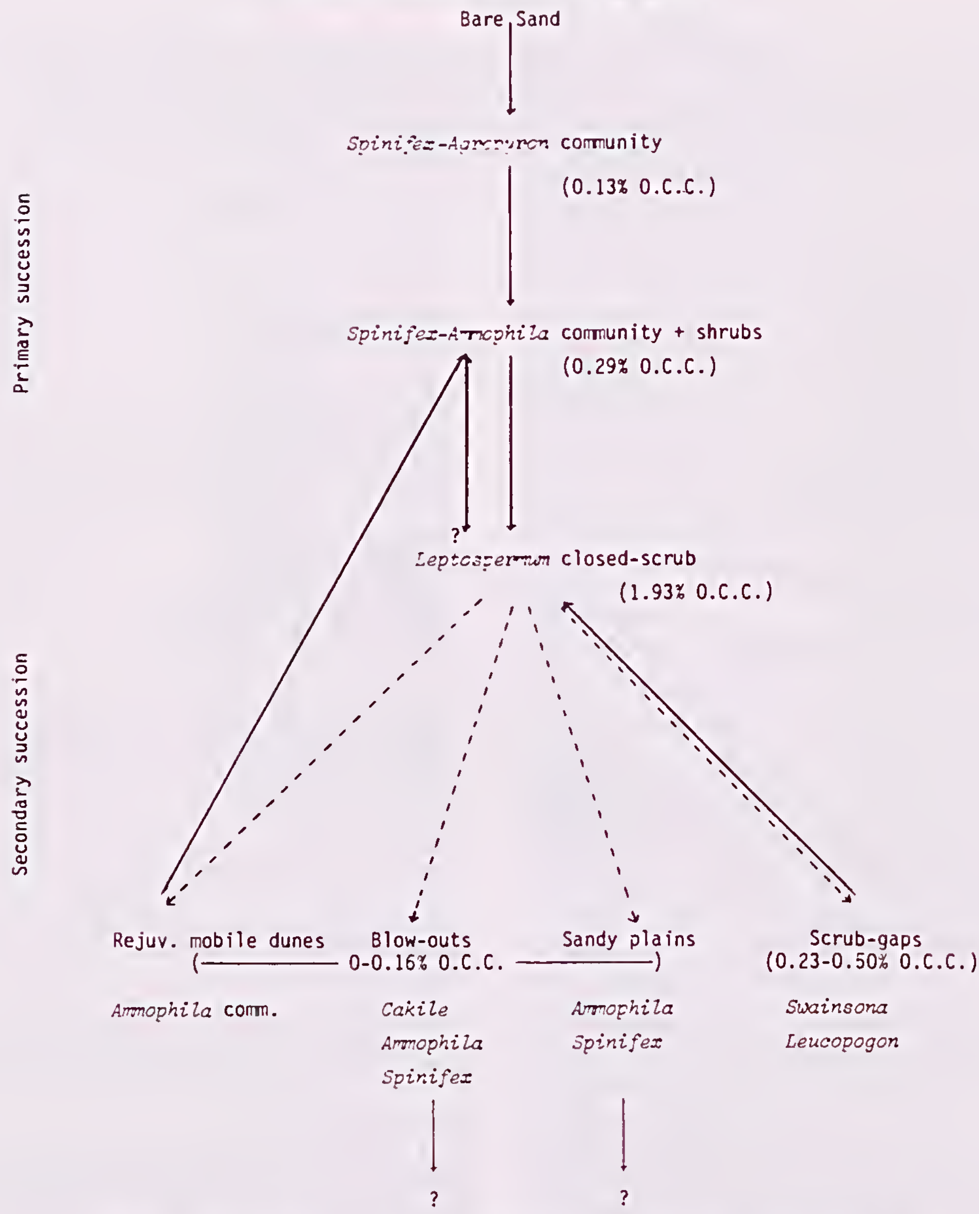

Fig. 4—Summary of types, pattern and direction of succession at Gunnamatta.

juvenated mobile dunes; (ii) Blow-outs; (iii) Sandy plains; and, (iv) Scrub-gaps. Of these, the first three have somewhat similar conditions in that the substratum is mobile (moderate to heavy deposition/erosion of sand), bare and low in organic matter. In all three, a change in pioneer colonizing species is observed; for example in mobile dunes, *Ammophila* has replaced *Spinifex*; in blow-outs and sandy plains the process of colonization appears to be extremely slow and in most places there is an assemblage of *Spinifex-Ammophila-Cakile* as pioneer plants.

As the first three units at Gunnamatta, especially (ii) and (iii), are still in the initial stages of colonization it would not be reasonable to predict the direction in which they will proceed, because this would, in all probability, be determined by several factors. The outstanding difference between these (i-iii) and scrub-gaps (iv) is in the type of colonizers. Scrub-gaps are singular in that early colonizers here are *Swainsona, Senecio* and *Leucopogon* rather than *Spinifex, Ammophila* and *Cakile*—not only in the early stages of primary succession but also in secondary succession. It seems likely that the principal factor to which this difference may be attributable is the type of substratum, which is relatively rich in organic matter and has greater stability. Like other sites of secondary succession at Gunnamatta,

TABLE 8

THE MEANS OF PERCENTAGE FREQUENCY (F) AND COVER (C) OF DIFFERENT SPECIES IN MAIN TOPOGRAPHIC UNITS AT GUNNAMATTA. MEANS ARE BASED ON DATA OF THREE SITES FOR ANY TOPOGRAPHIC UNIT.

	Front Initial Dune		Mobile Dune		Fixed Dune		Crater		Cleft	
	F	C	F	C	F	C	F	C	F	C
Acacia longifolia var. *sophorae*	–	–	–	–	3	+	–	–	11	4
Agropyron junceum	96	7	–	–	–	–	–	–	–	–
Ammophila arenaria										
(young plants)	19	2	51	13	–	–	–	–	–	–
(old plants)	–	–	–	–	52	9	7	2	25	3
Ancaena anserinifolia	–	–	–	–	2	+	–	–	2	+
Apium prostratum	–	–	–	–	3	+	–	–		
Cakile maritima	6	1	2	+	–	–	–	–	–	–
Calocephalus brownii	–	–	–	–	–	–	14	5	5	+
Carpobrotus aequilaterus	–	–	–	–	17	2	10	1	28	4
Clematis microphylla	–	–	–	–	9	1	–	–	10	+
Crassula sieberana	–	–	–	–	8	+	5	+	2	+
Festuca littoralis	6	1	–	–	–	–	5	+	–	–
Helichrysum paralium	3	1	–	–	10	2	17	3	18	7
Kennedia prostrata	–	–	–	–	–	–	–	–	3	+
Lagurus ovatus	–	–	–	–	57	3	20	1	69	4
Leptospermum laevigatum	–	–	–	–	10	2	2	1	11	8
Leucopogon parviflorus	–	–	–	–	24	4	8	3	33	7
Melilotus indica	–	–	–	–	59	5	67	4	60	5
Olearia axillaris	–	–	–	–	5	1	4	1	6	1
Orobanche minor	–	–	–	–	3	+	2	+	4	+
Pimelea serpyllifolia	–	–	–	–	16	2	7	1	29	4
Scirpus nodosus	–	–	–	–	18	3	34	4	42	4
Senecio lautus	3	+	–	–	33	2	23	1	28	2
Spinifex hirsutus										
(young plants)	84	14	6	1	–	–	–	–	–	–
(old plants)	–	–	–	–	50	10	42	7	23	3
Stackhousia spathulata	25	+	–	–	18	+	12	1	3	+
Swainsona lessertiifolia	–	–	–	–	3	+	5	+	7	+

\+ indicates less than 1% cover
– indicates absence of a species

scrub-gaps are at present only in a very early stage of colonization so that the future trend of succession is unclear. But since the habitat conditions and plant species here are comparable to the second stage of primary succession, it may be conjectured that primary and secondary succession will converge at this point. The pattern of primary succession at Gunnamatta is somewhat similar to that of other dune systems in Victoria (Turner, Carr & Bird 1962, Barson & Calder 1981) although the dominant species are different. More studies are required to assess the effects of disturbances in modifying the pattern of primary succession.

ACKNOWLEDGEMENTS

We thank National Parks Service for permission to work at Gunnamatta Beach, Mr O. R. Johnson for his help in computing and Professor M. J. Canny for providing the research facilities and his keen interest in this work. The assistance of Dr N. C. Sacheti is gratefully acknowledged. One of us (U.S.) received a Monash University Graduate Scholarship to carry out this project as part of her Ph.D. studies.

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